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Editorial: The evolutionary roots of reproductive ageing and reproductive health across the tree of life

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Editorial on the Research Topic

[The evolutionary roots of reproductive ageing and reproductive health across the tree of life](#)

Introduction

The last decades have seen a burst in the number of empirical studies documenting reproductive ageing (i.e. the decrease in reproductive performance with increasing age; also called reproductive senescence) under very diverse environmental conditions (e.g. in wild and captive populations). So far, most detailed investigations (and subsequent empirical evidence) of reproductive ageing patterns have been conducted on birds and mammals (Holmes et al., 2003; Nussey et al., 2013; Lemaître et al., 2020; Comizzoli and Ottinger, 2021), which is easily explained by the fact that, for a long time, most long-term individual-based longitudinal studies of populations in the wild focused on these Vertebrate classes (Clutton-Brock and Sheldon, 2010). However, empirical studies on other taxonomic groups have started to emerge, enabling us to broaden our understanding of the eco-evolutionary roots of reproductive ageing across the tree of life (see e.g. Crosland et al.; English et al.; Tully for three articles from this Research Topic documenting reproductive ageing in invertebrates, see next sections for details).

Reproductive ageing is often assumed to be negligible in species with indeterminate growth, because the increasing size of females throughout the entire life is expected to be associated with an increased fecundity (Jones and Vaupel, 2017). However, increased fecundity with age does not preclude ageing in other reproductive traits. In particular, a decrease in offspring performance with maternal age might counter-balance the fecundity increase and lead to lower reproductive success with increasing age (see Depeux et al., 2020 for a case study in the common pill woodlouse, *Armadillidium vulgare*). To date, empirical support for an absence of reproductive ageing in indeterminate growers is badly missing. In this Research Topic, Vrtilík et al. shed light on reproductive ageing patterns in indeterminate growers by compiling an impressive set of published case-studies on ray-finned fishes (*Actinopterygii*). They found evidence of reproductive ageing in 26% of studies, a figure that is likely

underestimated due to the short age range relative to reproductive lifespan that was covered in most studies. Reproductive ageing occurs in both sexes in a wide range of reproductive traits including breeding frequency and sperm quality. This study suggests that albeit variable among taxa, reproductive ageing does occur in indeterminate growers and is therefore likely more pervasive across the tree of life than generally assumed.

Despite this consistently increasing set of species displaying reproductive ageing, the eco-evolutionary causes and consequences of this process in terms of population dynamics and reproductive health remain to be fully deciphered. This Research Topic therefore brings together contributions whose common aim is to address the complexity of reproductive ageing through the lens of evolutionary biology, while using very different approaches, such as laboratory experiments, comparative analyses of ageing patterns across species, or the tracking of individual age-specific reproductive trajectories within populations in the wild.

Reproductive ageing and evolutionary theories of ageing

All evolutionary theories of ageing are rooted in the decrease of the force of selection when organisms age, leading to expect ageing to occur in all biological functions. However, most theoretical work has focused on the rate and shape of actuarial ageing (i.e. the increase in mortality risk with increasing age). For instance, the landmark work by Hamilton (1966) provides clear predictions for actuarial ageing and only briefly discuss reproductive ageing, stating that “*the problem seems to be biologically more complex than that concerning the mortalities*” (p. 42). This might explain why reproductive ageing has been much less studied than actuarial ageing until recently. The diversity of patterns even within a single taxonomic group (see e.g. Lemaître et al. (2020) for a comparative analysis across mammals) and the quite large number of traits involved in the sequential process of reproduction (Lemaître and Gaillard, 2017) support Hamilton’s view of the complexity of reproductive ageing. In this Research Topic, Lee and Chu, 2023 partly fill this knowledge gap by proposing an optimal life history model of ageing in fertility. Despite its simplicity, this model nicely captures the diversity of ageing patterns in fertility and shows that the life history strategies and the life styles, likely in an interplay with the environmental context, influence both the direction and the shape of fertility changes over age during the adulthood stage. The awareness that the environmental context markedly influences ageing patterns is growing, but we still lack a mechanistic understanding on how this might happen. Crosland et al.’s experimental work provides a highly relevant case study in that context using the mealworm beetle (*Tenebrio molitor*). They raised beetles under environments with highly contrasting quality by manipulating relative humidity conditions. They found that females raised in good conditions (i.e. high relative humidity) grew faster, lived longer, and produced more offspring over their lifetime than females raised in poor conditions (i.e. low relative humidity). On the other hand,

females raised in good conditions displayed a stronger reproductive ageing than females raised in poor conditions, providing a direct support for evolutionary theories predicting a trade-off between fast growth and high fecundity early in life and performance of fitness-related traits (reproductive output in that case) late in life (e.g. disposable soma theory, see Kirkwood and Rose, 1991).

Ageing in male’s fertilization efficiency

Compared to females, our current knowledge on male reproductive ageing is limited, especially regarding the effects of age on the efficiency at fertilizing eggs. Yet, male’s Darwinian fitness is often predominantly determined by fertilization success and one could thus easily predict that reproductive ageing in males should be primarily driven by a decline in the performance of ejaculate-related traits, such as sperm quality or sperm quantity, with increasing age. The ageing in male’s fertilization efficiency is nonetheless attracting lots of interest in public health studies, as the age at which fathers conceive offspring is continuously delayed in western societies. The wave of studies performed in that context have demonstrated that both sperm quality (e.g. sperm motility) and quantity (e.g. semen volume) show unambiguous evidence of ageing across human populations (Johnson et al., 2015). It is only recently that evolutionary biologists have started to investigate ageing in ejaculate-related traits. Yet, this process could have major consequences in terms of eco-evolutionary dynamics (Bonduriansky et al., 2008), especially in polyandrous or promiscuous species where sperm competition occurs (i.e. when ejaculates from different males compete to fertilize one or more oocytes, see Parker, 1970). So far, no consensus on the pervasive nature of ageing in ejaculate-related traits has been reached, simply because most of the studies performed in that context failed to encompass the full male reproductive life, which ultimately impact the likelihood to detect ageing (Sanghvi et al., 2023). Two empirical studies published in this Research Topic, both performed on birds, thoroughly embrace this topic (Meunier et al.; Míčková et al.). A third (Fricke et al.), very complementary to the previous ones, focus on the putatively widespread ageing of the seminal fluid content (i.e. non-fertilizing part of the ejaculate).

Using artificial insemination experiments in North African houbara bustard (*Chlamydotis undulata undulata*), Meunier et al. disentangle the influence of pre-meiotic ageing (i.e. effects due to male’s age) and post-meiotic ageing (i.e. effects due to sperm’s age) on diverse sperm features and reproductive success metrics. They document a marked decline in both quantity (i.e. ejaculate volume, sperm concentration) and quality (i.e. motility, velocity) with increasing male’s age, which ultimately translate into the hatching of chicks displaying lower growth rates and higher mortality rate. Unexpectedly, the sperm age has a positive influence on both sperm quality traits and hatching success.

Focusing on pre-meiotic sperm ageing in a population of barn swallow (*Hirundo rustica rustica*) intensively monitored during a longitudinal study, Míčková et al. provide a thorough analysis of the age-specific changes in diverse sperm characteristics over the male’s life course. While their analyses reveal a decline in sperm length

with increasing age, both sperm velocity and sperm production intensity (assessed by the size of the cloacal protuberance) show no sign of ageing. Interestingly, the authors also document a negative association between the size of the cloacal protuberance and lifespan occurs among males, suggesting potential survival costs of maintaining high levels of sperm production throughout the life.

Finally, Fricke et al. provide the first qualitative review of the effect of male's age on seminal fluid content. Indeed, male's reproductive success is also mediated by the non-fertilizing part of the ejaculates (Perry et al., 2013), especially by the seminal fluid proteins produced by the accessory reproductive glands. These proteins typically interact with sperm cells or modulate female's reproductive behavior to increase male's fertilization success (e.g. Chapman et al., 2003). Everything else being equal, any decline in the quality of the seminal fluid should impair male's reproductive success. Fricke et al. compile fourteen papers reporting an effect of male's age on seminal fluid proteins. Their review highlights contrasted patterns among studies (e.g. from a decrease to an increase in the concentration of some proteins) possibly caused by major methodological issues such as a too short age range covered relative to reproductive lifespan (see also above) or an absence of control for prior mating experiences.

The asynchrony between reproductive and non-reproductive ageing

One salient challenge currently associated with the study of reproductive ageing is the need to embrace the sequential nature of reproduction. In both sexes, reproductive success (i.e. the number of offspring produced by a female and alive at the end of the parental care period) involves a sequence of events (e.g. implantation success, birth success in females, pre- and post-copulatory competition in males) underpinned by phenotypic traits (size of secondary sexual traits) and physiological functions (e.g. milk production, spermatogenesis) that can all decline with increasing age (Lemaître and Gaillard, 2017). Similar observations have been made for other phenotypic traits (e.g. physiological or behavioural traits) - not directly linked with reproduction - that all seem to follow their own age-specific trajectory (Promislow et al., 2006; Gaillard and Lemaître, 2017). However, despite theoretical predictions (Williams, 1957; Maynard Smith, 1962; Moorad and Ravindran, 2022), the magnitude of the asynchrony in ageing among reproductive traits (and beyond) is yet to be quantified and the role of natural selection in shaping this mosaic pattern of ageing remains to be empirically tested. Two articles published in this Research Topic directly address these questions (Moulllec et al.; Tully).

Taking advantage of the long-term studies of two Alpine swift (*Tachymarptis melba*) colonies, Moulllec et al. performed a thorough analysis of ageing patterns in both sexes across eleven phenotypic and life history traits, including notably four reproductive traits (i.e. laying date, clutch size, brood size at hatching and at fledgling). Their analyses highlight marked differences in age-specific patterns among traits and between

sexes. For instance, among females, tail length shows a late age at the onset of ageing (ca. 15 years of age) while the brood size at hatching starts to decline earlier (ca. 12 years of age), but at a much lower rate. These findings indicate differences between reproductive and somatic ageing. Interestingly, when focusing strictly on reproductive traits, ageing is detected only in brood size at hatching and at fledgling and only in males, an intriguing result further discussed in the context of sex-differences in life history tactics.

Differences between actuarial and reproductive ageing patterns are also at the core of the study by Tully focusing on *Collembola (Folsomia candida)* lineages originating from two phylogenetically distinct clades. This study reveals a clear decline in clutch size with increasing age, with quite marked differences in both onset and rate of reproductive ageing among clades and experimental treatments. However, for most clades, the onset of reproductive ageing in clutch size is earlier than the onset of actuarial senescence. On the other hand, ageing in egg's size seems to be negligible, a result consistent across all lineages. In addition, *Collembola* under a dietary restriction regime show a delayed onset of reproductive ageing, as well as a lower rate of reproductive ageing, a finding discussed at the light of recent advances in the study of phenotypic plasticity in ageing.

The influence of environmental conditions on reproductive ageing

There is increasing evidence that the intensity of ageing is influenced by either current or past environmental conditions. For instance, mammals from species with a short generation time display a delayed and weaker actuarial ageing in zoos than in the wild, leading captive individuals to outlive markedly their conspecifics in the wild (Tidière et al., 2016). On the other hand, poor early-life conditions did not have detectable effects on actuarial ageing from the meta-analysis performed by Cooper and Kruuk (2018). The figure for reproductive ageing seems to be different although the influence of current conditions on reproductive ageing has been less investigated on reproductive ageing than on actuarial ageing. In this Research Topic, two studies provide clear evidence for an influence of current environmental conditions on reproductive ageing. Naciri et al. perform a detailed analysis of reproductive ageing in polar bears (*Ursus maritimus*) in the intensively monitored population of Svalbard. They provide clear evidence of reproductive ageing in both litter production and litter size, which decline slightly for females aged 15-20 years and markedly from 20 years of age onwards. On the other hand, neither offspring mass or survival within the maternal care period display any evidence of reproductive ageing. Although the response of reproductive ageing metrics to variation in environmental conditions is not investigated, the authors provide clear evidence that older females are more susceptible to environmental harshness (measured by the date of sea-ice break-up) than prime-aged ones, suggesting that ageing is more pronounced under harsh environmental conditions. Likewise, Kappeler et al. compare reproductive ageing between wild and captive conditions in

two lemur taxa (Verreaux's sifakas, *Propithecus verreauxi* and redfronted lemurs, *Eulemur rufifrons*). They provide consistent evidence of reproductive ageing (although not statistically significant for one population in the wild likely because of a lack of statistical power), supporting again the view that reproductive ageing is the rule rather than the exception in mammals (Lemaître et al., 2020). The intensity of reproductive ageing differs between captive and wild conditions. Interestingly, the decrease of reproductive performance with increasing age is delayed and less steep in the wild than under captive conditions, while the opposite generally occurs for actuarial senescence (Tidière et al., 2016). This discrepancy likely involves husbandry decisions as mating patterns are generally controlled by managers in captive populations of large mammals. These findings provide new evidence for variable ageing patterns within a same species in response to different environmental contexts.

Previous studies indicate that early-life conditions seem to be influential on the intensity of reproductive ageing. Thus, in their meta-analysis, Cooper & Kruuk (2018) provided evidence of early-life effects on reproductive ageing (see also Nussey et al., 2007 for a convincing example in red deer, *Cervus elaphus*). Two case studies in this Research Topic test whether early-life conditions shape reproductive ageing. Taking advantage from the long-term monitoring of male antlers in two roe deer (*Capreolus capreolus*) populations facing with markedly different environmental conditions, Cambreling et al. document a decrease of antler size with increasing age from 7 years of age onwards irrespective of the population, which supports the occurrence of reproductive ageing in males. Moreover, in both populations, ageing in antler length is delayed for males born in good cohorts (i.e. heavy when 8 months of age) compared to those born in poor cohorts (i.e. light when 8 months of age), which supports the influence of early-life conditions on reproductive ageing and indicates that male antler size is a honest signal of phenotypic quality. From an experimental approach, Vedder et al. assess the influence of early-life conditions on performance later in life using a captive population of Japanese quail (*Coturnyx japonica*). They used the incubation temperature (normal vs. cool) to mimic variation in the quality of early-life conditions. The reproductive performance (measured by the daily laying rate) declines markedly with increasing female age, supporting reproductive ageing. However, early-life conditions do not have any detectable influence on reproductive ageing, and more generally on any adult life history trait. Although these findings might suggest that incubation temperature is not an important driver of early-life conditions, they are also in line with the general observation that mild environments such as that provided for captive female quails in this study decrease the intensity of reproductive ageing, and thereby the magnitude of silver spoon (sensu Grafen, 1988) or carry-over (see Harrison et al., 2011) effects.

From reproductive ageing to reproductive health

A substantial variation in both the onset and the rate of reproductive ageing has been reported within species (Gaillard

and Lemaître, 2020) and the multiple pathologies that can impact the reproductive machinery could potentially contribute to the pronounced reproductive ageing observed in some males and females. However, the influence of past and current reproductive diseases on reproductive ageing has almost never been quantified and the eco-evolutionary roots of such diseases are yet to be fully deciphered (but see Alvarado, 2013; Jasienska, 2013). Similarly, it is largely unknown to what extent the risk of diseases (and in particular, reproductive diseases) has, in a given environment, influenced the evolution of age-specific reproductive tactics. Three articles from this Research Topic shed a new light on these questions.

In a perspective paper, Dujon et al. explore the untapped associations between age-specific reproductive allocation (including reproductive ageing) and cancer risk. These authors first provide an overview of the possible evolutionary trade-offs linking age-specific fertility and cancer risk, by notably focusing on genes with pleiotropic and antagonistic effects. They go beyond the classic examples of *Xmrk* melanoma-promoting oncogene in fish or the more controversial BRCA1 and BRCA2 alleles in humans by questioning the potential pivotal role of genes controlling gamete production in the context of cancer risk. Then, they review the multiple and complex relationships that putatively link the allocation of resources towards sexual competition and reproduction over the life course to the evolution of cancer-defense mechanisms and elaborate on the selective forces played by cancer risk on the evolution of reproductive ageing.

In line with the review from Dujon et al., Bieuville et al. further explore the association between women's reproductive history and post-menopausal health by investigating the life history determinants of breast cancer risk. More specifically, they reveal that postmenopausal breast cancer risk is higher in the subset of women who experienced the highest number of lifetime menses. In addition, an elevated number of menses also appears to be associated with an earlier onset of breast cancer after menopause. These results are discussed in the context of an evolutionary mismatch where the rapid increase in number of menses through women's recent evolutionary history is responsible for a higher lifetime exposure to cyclic reproductive hormones (e.g. progesterone), which triggers the risk of developing breast cancer. This study thus emphasizes the tight link between age-specific reproductive effort and reproductive health and calls for further work testing how the association between reproductive effort in early life and reproductive ageing (e.g. Nussey et al., 2006) might be mediated by reproductive health issues.

Finally, English et al. extend the range of reproductive traits that are traditionally analyzed in reproductive ageing studies by focusing on a key public health issue: the abortion rate. Using the long-lived tsetse fly (*Glossina morsitans morsitans*) as a biological model, they document a higher rate of abortion in old females compared to middle-age females at both late-larval stage and egg-stage. Importantly, this increase in reproductive loss in late life does not appear to be adaptive as it does not reduce the interval of time before the next laying event nor increase the body mass of the future offspring. This study further demonstrates that abortion rates increase under harsh environment and thus calls for additional studies investigating both the occurrence and the magnitude of this

reproductive process, largely neglected in the evolutionary biology literature.

Concluding remarks: exploring the genetic and physiological basis of reproductive ageing

The content of this Research Topic clearly demonstrates the lively nature of the current research performed in the field of reproductive ageing. Moreover, it highlights that deciphering the eco-evolutionary roots of reproductive ageing as well as its consequences in terms of both population dynamics and public health require inputs from many research areas. It is also important to emphasize that the topic explored by the various contributions included in this Research Topic are only the tip of the iceberg, and other salient research questions on reproductive ageing need to be tackled in the near future. Among them, we can notably mention the quantification of the amount of individual heterogeneity in both the onset and rate of reproductive ageing but also the identification of the physiological and genetic markers of reproductive ageing in wild animal populations. Regarding the latter, the study from Meyer *et al.* published in this Research Topic paves the road for such research projects. Here, taking advantage of a long-term individual based study in common tern (*Sterna hirundo*), these authors explore the age-related changes in autosomal methylation for both males and females in this population. The key role that epigenetic changes (hyper- or hypo- methylation) plays on ageing is currently attracting lots of interest (e.g. Lu *et al.*, 2023) and their analyses reveal that autosomal methylation levels decline with increasing age in females, but not in males. However, as emphasized by Meyer *et al.* senescence patterns do not differ between sexes in common terns, which highlight that the association between age-specific changes in epigenetic profiles and

ageing, notably reproductive ageing, is complex and requires further investigations.

Author contributions

JL: Conceptualization, Writing – original draft, Writing – review & editing. JG: Conceptualization, Writing – original draft, Writing – review & editing.

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